Developmental Biology

An International Journal Published under the Auspices of the Society for Developmental Biology

Editor-in-Chief: PETER J. BRYANT

Associate Editors

Eileen D. Adamson
Merton Bernfield
Ira B. Black
Connie J. Eaves
Scott E. Fraser
John C. Gerhart
Stephen Hauschka
H. Robert Horvitz
Laurinda A. Jaffe
Story C. Landis
William F. Loomis
Carl N. McDaniel
Anne McLaren
Elliot Meyerowitz
Bjorn R. Olsen
Bruce M. Paterson
Ralph Quatrano
Rudolf A. Raff
Janet Rossant
Matthew Scott
James W. Truman
Victor D. Vacquier
Lawrence J. Wangh
Fred Wilt
Lewis Wolpert

Editorial Assistant: Jayne M. Sutton

Review Article Editor: Anthony P. Mahowald

VOLUME 133, 1989

ACADEMIC PRESS, INC.

San Diego New York Boston London Sydney Tokyo Toronto

Copyright © 1989 by Academic Press, Inc.

All Rights Reserved

No part of this publication may be reproduced or transmitted in any form, or by any means, electronic or mechanical, including photocopy, recording, or any information storage and retrieval system, without permission in writing from the copyright owner.

The appearance of the code at the bottom of the first page of an article in this journal indicates the copyright owner's consent that copies of the article may be made for personal or internal use, or for the personal or internal use of specific clients. This consent is given on the condition, however, that the copier pay the stated per copy fee through the Copyright Clearance Center, Inc. (27 Congress Street, Salem, Massachusetts 01970), for copying beyond that permitted by Sections 107 or 108 of the U.S. Copyright Law. This consent does not extend to other kinds of copying, such as copying for general distribution, for advertising or promotional purposes, for creating new collective works, or for resale. Copy fees for pre-1989 articles are as shown on the article title pages; if no fee code appears on the title page, the copy fee is the same as for current articles.

0012-1606/89 $3.00

MADE IN THE UNITED STATES OF AMERICA

Contents of Volume 133

NUMBER 1, MAY 1989

Full Papers

TRENT D. STEPHENS, RAFAEL L. W. BEIER, DIRK C. BRINGHURST, SCOTT R. HIATT, MOZELLE PRESTRIDGE, DOUGLAS E. PUGMIRE, AND HOWARD J. WILLIS. Limbness in the Early Chick Embryo Lateral Plate 1

C. G. BELLOWS AND J. E. AUBIN. Determination of Numbers of Osteoprogenitors Present in Isolated Fetal Rat Calvaria Cells *in Vitro* 8

BRUCE J. DRAGER, MICHAEL A. HARKEY, MINEO IWATA, AND ARTHUR H. WHITELEY. The Expression of Embryonic Primary Mesenchyme Genes of the Sea Urchin, *Strongylocentrotus purpuratus*, in the Adult Skeletogenic Tissues of This and Other Species of Echinoderms 14

LEA HIRAOKA, WENDY GOLDEN, AND TERRY MAGNUSON. Spindle-Pole Organization during Early Mouse Development 24

LYNN A. DAVIS, ROY C. OGLE, AND CHARLES D. LITTLE. Embryonic Heart Mesenchymal Cell Migration in Laminin 37

J. DAVID MOURY AND ANTONE G. JACOBSON. Neural Fold Formation at Newly Created Boundaries between Neural Plate and Epidermis in the Axolotl 44

LAURENT MEIJER, W. DOSTMANN, H. G. GENIESER, E. BUTT, AND BERND JASTORFF. Starfish Oocyte Maturation: Evidence for a Cyclic AMP-Dependent Inhibitory Pathway 58

NOBUAKI MAEDA, MICHIO NIINOBE, YOSHIRO INOUE, AND KATSUHIKO MIKOSHIBA. Developmental Expression and Intracellular Location of P_{400} Protein Characteristic of Purkinje Cells in the Mouse Cerebellum 67

TOSHITAKA FUJISAWA. Role of Interstitial Cell Migration in Generating Position-Dependent Patterns of Nerve Cell Differentiation in *Hydra* 77

STUART B. MOSS, PETER B. CHALLONER, AND MARK GROUDINE. Expression of a Novel Histone 2B during Mouse Spermiogenesis 83

PAUL A. KRIEG, SUSAN M. VARNUM, W. MICHAEL WORMINGTON, AND DOUG A. MELTON. The mRNA Encoding Elongation Factor 1-α (EF-1α) Is a Major Transcript at the Midblastula Transition in *Xenopus* 93

TATSUO S. HAMAZAKI, YOSHITAKA NAGAHAMA, ICHIRO IUCHI, AND KENJIRO YAMAGAMI. A Glycoprotein from the Liver Constitutes the Inner Layer of the Egg Envelope (Zona Pellucida Interna) of the Fish, *Oryzias latipes* 101

VICTOR D. VACQUIER, DONALD C. PORTER, STEVEN H. KELLER, AND MILO AUKERMAN. Egg Jelly Induces the Phosphorylation of Histone H3 in Spermatozoa of the Sea Urchin *Arbacia punctulata* 111

MIKA SATO AND YASUJI SAWADA. Regulation in the Numbers of Tentacles of Aggregated Hydra Cells 119

JANE A. LANGDALE, BARBARA LANE, MICHAEL FREELING, AND TIMOTHY NELSON. Cell Lineage Analysis of Maize Bundle Sheath and Mesophyll Cells 128

G. FERRARI, M.-C. MINOZZI, G. TOFFANO, A. LEON, AND S. D. SKAPER. Basic Fibroblast Growth Factor Promotes the Survival and Development of Mesencephalic Neurons in Culture 140

CHRISTOPHER E. KILLIAN AND FRED H. WILT. The Accumulation and Translation of a Spicule Matrix Protein mRNA during Sea Urchin Embryo Development 148

ROBERT SAVAGE AND CAREY R. PHILLIPS. Signals from the Dorsal Blastopore Lip Region during Gastrulation Bias the Ectoderm toward a Nonepidermal Pathway of Differentiation in *Xenopus laevis* 157

HÉLÈNE RIME, ISABELLE NEANT, PIERRE GUERRIER, AND RENE OZON. 6-Dimethylaminopurine (6-DMAP), A Reversible Inhibitor of the Transition to Metaphase during the First Meiotic Cell Division of the Mouse Oocyte 169

JOHANNA E. SPEKSNIJDER, LIONEL F. JAFFE, AND CHRISTIAN SARDET. Polarity of Sperm Entry in the Ascidian Egg 180

MOHINDER K. BANSAL, ALLYSON S. A. ROSS, AND JONATHAN B. L. BARD. Does Chondroitin Sulfate Have a Role to Play in the Morphogenesis of the Chick Primary Corneal Stroma? 185

RICHARD W. BEEMAN, JEFFREY J. STUART, M. SUSAN HAAS, AND ROBIN E. DENELL. Genetic Analysis of the Homeotic Gene Complex (HOM-C) in the Beetle *Tribolium castaneum* ... 196
FAZAL M. MANEJWALA, EDWARD J. CRAGOE, JR., AND RICHARD M. SCHULTZ. Blastocoel Expansion in the Preimplantation Mouse Embryo: Role of Extracellular Sodium and Chloride and Possible Apical Routes of Their Entry ... 210
SUE A. MCDONALD AND ROCKY S. TUAN. Expression of Collagen Type Transcripts in Chick Embryonic Bone Detected by *in Situ* cDNA-mRNA Hybridization ... 221
JEANNE BENTLEY LAWRENCE, KRISHAN TANEJA, AND ROBERT H. SINGER. Temporal Resolution and Sequential Expression of Muscle-Specific Genes Revealed by *in Situ* Hybridization ... 235
FRANÇOIS X. OMLIN AND JOCELYNE WALDMEYER. Differentiation of Neuron-like Cells in Cultured Rat Optic Nerves: A Neuron or Common Neuron-Glia Progenitor? ... 247
S. A. H. HOFFMEISTER. Action of Foot Activator on Growth and Differentiation of Cells in Hydra ... 254
LORENZ T. H. RAMSEYER, JANET BARKER-HARREL, DAVID J. SMITH, KARI A. MCBRIDE, ROBERT N. JARMAN, AND ROBERT H. BROYLES. Intracellular Signals for Developmental Hemoglobin Switching ... 262
EVERARDUS J. J. VAN ZOELEN, THEODORA M. J. WARD-VAN OOSTWAARD, RIENK NIEUWLAND, BART VAN DER BURG, ADRIANA J. M. VAN DEN EIJNDEN-VAN RAAIJ, CHRISTINE L. MUMMERY, AND SIEGFRIED W. DE LAAT. Identification and Characterization of Polypeptide Growth Factors Secreted by Murine Embryonal Carcinoma Cells ... 272
LEONORA J. REGENSTREIF AND JANET ROSSANT. Expression of the c-*fms* Proto-oncogene and of the Cytokine, CSF-1, during Mouse Embryogenesis ... 284
SHIGEAKI KURASAWA, RICHARD M. SCHULTZ, AND GREGORY S. KOPF. Egg-Induced Modifications of the Zona Pellucida of Mouse Eggs: Effects of Microinjected Inositol 1,4,5-Trisphosphate ... 295

Brief Notes
ROSELLA COLONNA, SANDRA CECCONI, CARLA TATONE, FRANCO MANGIA, AND ROBERTO BUCCIONE. Somatic Cell-Oocyte Interactions in Mouse Oogenesis: Stage-Specific Regulation of Mouse Oocyte Protein Phosphorylation by Granulosa Cells ... 305
M. MALLAT, R. HOULGATTE, P. BRACHET, AND A. PROCHIANTZ. Lipopolysaccharide-Stimulated Rat Brain Macrophages Release NGF *in Vitro* ... 309
Features ... f-1

NUMBER 2, JUNE 1989

Full Papers
CHERYL L. COURCHESNE-SMITH AND SARA L. TOBIN. Tissue-Specific Expression of the 79B Actin Gene during *Drosophila* Development ... 313
D. ASSELINEAU, B. A. BERNARD, C. BAILLY, AND M. DARMON. Retinoic Acid Improves Epidermal Morphogenesis ... 322
CLAIRE KREMEN. Patterning during Pupal Commitment of the Epidermis in the Butterfly, *Precis coenia:* The Role of Intercellular Communication ... 336
HENRI GOUDEAU AND MARIE GOUDEAU. A Long-Lasting Electrically Mediated Block, Due to the Egg Membrane Hyperpolarization at Fertilization, Ensures Physiological Monospermy in Eggs of the Crab *Maia squinado* ... 348
L. J. SWEENEY, J. M. KENNEDY, R. ZAK, K. KOKJOHN, AND S. W. KELLEY. Evidence for Expression of a Common Myosin Heavy Chain Phenotype in Future Fast and Slow Skeletal Muscle during Initial Stages of Avian Embryogenesis ... 361
LYNN M. WILEY AND MICHAEL FEMI OBASAJU. Effects of Phlorizin and Ouabain on the Polarity of Mouse 4-Cell/16-Cell Stage Blastomere Heterokaryons ... 375
PATRICIO MORALES, NICHOLAS L. CROSS, JAMES W. OVERSTREET, AND FREDERICK W. HANSON. Acrosome Intact and Acrosome-Reacted Human Sperm Can Initiate Binding to the Zona Pellucida ... 385
MARY BLAIR CLARK AND MARY BARTLETT BUNGE. Cultured Schwann Cells Assemble Normal-Appearing Basal Lamina only when They Ensheathe Axons ... 393
HIROSHI ANDO, YASUJI SAWADA, HIROSHI SHIMIZU, AND TSUTOMU SUGIYAMA. Pattern Formation in Hydra Tissue without Developmental Gradients ... 405
P. FERRETTI, D. M. FEKETE, M. PATTERSON, AND E. B. LANE. Transient Expression of Simple Epithelial Keratins by Mesenchymal Cells of Regenerating Newt Limb ... 415

CHRISTIAN KLÄMBT, STEPHAN MÜLLER, REINHARD LÜTZELSCHWAB, RITA ROSSA, FRANK TOTZKE, AND OTTO SCHMIDT. The *Drosophila melanogaster l(2)gl* Gene Encodes a Protein Homologous to the Cadherin Cell-Adhesion Molecule Family 425
DAVID W. RAIBLE AND F. ARTHUR MCMORRIS. Cyclic AMP Regulates the Rate of Differentiation of Oligodendrocytes without Changing the Lineage Commitment of Their Progenitors 437
WAYNE R. SPRINGER. Developmentally Regulated Cell-Cell Adhesion in *Dictyostelium purpureum* Is Mediated by a Glycoprotein Synthesized in Nonadhesive Cells 447
NIRUPA CHAUDHARI AND KURT G. BEAM. The Muscular Dysgenesis Mutation in Mice Leads to Arrest of the Genetic Program for Muscle Differentiation 456
RONALD W. OPPENHEIM, TOBY COLE, AND DAVID PREVETTE. Early Regional Variations in Motoneuron Numbers Arise by Differential Proliferation in the Chick Embryo Spinal Cord 468
MANUEL P. MARK, WILLIAM T. BUTLER, AND JEAN-VICTOR RUCH. Transient Expression of a Chondroitin Sulfate-Related Epitope during Cartilage Histomorphogenesis in the Axial Skeleton of Fetal Rats 475
ULF HEDIN, BRADFORD A. BOTTGER, JOHAN LUTHMAN, STAFFAN JOHANSSON, AND JOHAN THYBERG. A Substrate of the Cell-Attachment Sequence of Fibronectin (Arg-Gly-Asp-Ser) Is Sufficient to Promote Transition of Arterial Smooth Muscle Cells from a Contractile to a Synthetic Phenotype 489
P. GRANT AND Y. TSENG. *In Vitro* Growth Properties of *Xenopus* Retinal Neurons Undergo Developmental Modulation 502
DAVID J. KLEIN, DAVID M. BROWN, ANTOINETTE MORAN, THEODORE R. OEGEMA, JR., AND JEFFREY L. PLATT. Chondroitin Sulfate Proteoglycan Synthesis and Reutilization of β-D-Xyloside-Initiated Chondroitin/Dermatan Sulfate Glycosaminoglycans in Fetal Kidney Branching Morphogenesis 515
M. A. SATRE AND D. M. KOCHHAR. Elevations in the Endogenous Levels of the Putative Morphogen Retinoic Acid in Embryonic Mouse Limb-Buds Associated with Limb Dysmorphogenesis 529
LEONARD D. BOGARAD, MANUEL F. UTSET, ALEXANDER AWGULEWITSCH, TETSURO MIKI, CHARLES P. HART, AND FRANK H. RUDDLE. The Developmental Expression Pattern of a New Murine Homeo Box Gene: Hox-2.5 537
JEFFREY A. KAZZAZ AND CHARLES E. ROZEK. Tissue-Specific Expression of the Alternately Processed *Drosophila* Myosin Heavy-Chain Messenger RNAs 550
GARY P. RADICE AND GEORGE M. MALACINSKI. Expression of Myosin Heavy Chain Transcripts during *Xenopus laevis* Development 562
BRIAN S. SPOONER, KENNETH E. BASSETT, AND BRIAN S. SPOONER, JR. Embryonic Salivary Gland Epithelial Branching Activity Is Experimentally Independent of Epithelial Expansion Activity 569
BEATRIZ GONZALEZ-YANES, R. B. MANDELL, M. GIRARD, S. HENRY, O. APARICIO, M. GRITZALI, R. D. BROWN, JR., GREGORY W. ERDOS, AND CHRISTOPHER M. WEST. The Spore Coat of a Fucosylation Mutant in *Dictyostelium discoideum* 576
WILLIAM T. POUEYMIROU AND RICHARD M. SCHULTZ. Regulation of Mouse Preimplantation Development: Inhibition of Synthesis of Proteins in the Two-Cell Embryo That Require Transcription by Inhibitors of cAMP-Dependent Protein Kinase 588

Brief Notes

PETER J. CLEAVINGER, JAMES W. MCDOWELL, AND KAREN L. BENNETT. Transcription in Nematodes: Early *Ascaris* Embryos Are Transcriptionally Active 600
FRASER SHILLING, KAZUYOSHI CHIBA, MOTONORI HOSHI, TAKEO KISHIMOTO, AND LAURINDA A. JAFFE. Pertussis Toxin Inhibits 1-Methyladenine-Induced Maturation in Starfish Oocytes 605
MICHIKO TAKAGI SAWADA, TETSUYA SOMENO, MOTONORI HOSHI, AND HITOSHI SAWADA. Inhibition of Starfish Oocyte Maturation by Leupeptin Analogs, Potent Trypsin Inhibitors 609
PHYLLIS LUVALLE, MASANDO HAYASHI, AND BJØRN R. OLSEN. Transcriptional Regulation of Type X Collagen during Chondrocyte Maturation 613

Author Index for Volume 133 617

Cumulative Author Index for Volumes 131–133 619

Cumulative Subject Index for Volumes 131–133 622

Cumulative Organism Index for Volumes 131–133 641

Features f-1

Information for Authors

Developmental Biology will publish papers containing new and significant information bearing on developmental mechanisms of general interest. Analysis of development, growth, regeneration, and tissue repair in plants and animals at the molecular, cellular, and genetic levels are topics suitable for the journal. In all areas, analytic rather than descriptive studies will be favored.

Original papers only will be considered. Submission of a manuscript implies the authors' assurance that the same work has not been and will not be nor is presently submitted elsewhere, and that its submission for publication has been approved by all of the authors and by the institution where the work was carried out; further, that any person cited as a source of personal communications has approved such citation. Explicit proof of these implied assurances may be required at the Editor's discretion. Articles and any other material published in *Developmental Biology* represent the opinions of the author(s), and should not be construed to reflect the opinions of the Editor, the Publisher, or the Society for Developmental Biology.

Publication of a research article in *Developmental Biology* is taken to imply that the authors are prepared to distribute freely to interested academic researchers for their own use any clone (of cells or DNA or antibodies) used in the experiments reported. Manuscripts that report research involving human subjects must be supported by a copy of the document authorizing the proposed research, issued and signed by the appropriate official(s) of the institution where the work was conducted.

Authors submitting a manuscript do so on the understanding that if it is accepted for publication, copyright in the article, including the right to reproduce the article in all forms and media, shall be assigned exclusively to the Publisher. The Publisher will not refuse any reasonable request by the author for permission to reproduce any of his or her contributions to the journal.

Articles usually do not exceed 15,000 words and must be preceded by an abstract of about 200 words that should be fully intelligible by itself. Brief notes are 1500 words or less, including the bibliography, and should have an abstract of less than 100 words and a limit of one page of figures. All papers will be published in English.

Review and memorial articles are published after specific invitations from the editorial board; they are subject to the same review process as regular articles, but receive priority for publication. These articles are limited to 3000 words.

Manuscripts should be as concise as possible; full documentation of results should be combined with maximum brevity and clarity. Quantitative data should be presented so that the reader can readily judge statistical significance of differences. The discussion section should relate the present work to previous knowledge but should not be expanded into a review of the field. The standard order of sections is: abstract, introduction, materials and methods, results, and discussion. Combined results and discussion may be used. Acknowledgment, references, footnotes, tables, and figure legends should follow the discussion in that order. Number all manuscript pages consecutively and type double-spaced throughout. Provide a running title of 35 or fewer letters and spaces. Use footnotes sparingly; cite them with superscript numbers; type them on a separate sheet. Do not italicize for emphasis.

Abbreviations and units should be used consistently. Consult the lists published in the *Proceedings of the National Academy of Sciences (USA)*, the *Journal of Biological Chemistry*, and *Biochemistry* for standard abbreviations which need not be defined. Collect all abbreviations into a footnote and refer to it at the first use of an abbreviation. The use of units should follow the Système International. Use prefixes, e.g., μM, not 10^{-6} *M*. Note that *M* stands for molar, not mole. Use hr, min, sec, rpm, and cpm without definition, without a period, and without an "s" in the plural (i.e., 20 min).

Figures should be numbered consecutively in the order of their appearance and each should have a descriptive legend. Mark all figures with the orientation and with the authors' names. *Line drawings* will be reduced in accordance with the complexity of the figures. Good quality prints are acceptable. The maximum size submitted should be 215 × 280 mm. *Photographs* should be submitted as actual size for reproduction, fitting column (90 mm) or page (185 mm) width. Sets of micrographs mounted on light cardboard and in combinations up to 203 × 267 mm in size are acceptable. For best reproduction, provide clear, glossy prints with adequate contrast. The magnification should be indicated by a bar on the photograph. Figures that are to appear together as one plate should have comparable contrast and density and should be mounted on cardboard or paper as close together as possible. Do not combine line drawings and halftones into composite plates; if you wish them to appear together, submit unmounted original art and a layout sheet. The printer will place thin white lines between the figures on each plate. Providing an overlay that indicates the most critical areas of the micrograph will aid in ensuring high-quality reproduction.

Suggestions for *cover photographs* are welcome. Submit them as $8\frac{1}{2} \times 11$-inch color or black-and-white prints to accompany specific articles. A short (one-line) legend should accompany each photograph. *Illustrations in color* can be accepted only if the authors defray the cost; however, authors may apply to the Editor for financial assistance for this purpose.

Tables should be typed on separate pages and numbered consecutively with Arabic numerals; each should have a concise heading.

References to the literature should be cited as: Doe (1987) has observed that . . . ; (Doe, 1988). Doe *et al.* (1988) should be used in the case of articles with more than two authors. Use suffixes a, b, etc., following the date to distinguish two or more works by the same authors in the same year (Doe, 1987a,b). Arrange literature citations in the bibliography according to the surname of the author, using the following styles:

> COLIN, A. M. (1986). Rapid repetitive microinjection. *In* "Methods in Cell Biology" (T. E. Schroeder, Ed.), Vol. 27, pp. 395–406. Academic Press, San Diego, CA.
>
> HOLLEY, J. A., and SILVER, J. (1987). Growth pattern of pioneering chick spinal cord axons. *Dev. Biol.* **123,** 375–388.

Abbreviate journal titles according to *Chemical Abstracts Service Source Index*, 1985. Do not refer to abstracts or papers which have not been accepted for publication.

Proofs and Reprints. Proofs will be sent to the authors with reprint order forms. Fifty reprints of each article are provided free of charge. Additional reprints may be ordered using the form provided.

To submit a manuscript, send two complete copies including illustrations to Peter J. Bryant, Editor-in-Chief, *Developmental Biology*, Developmental Biology Center, University of California, Irvine, California 92717. Telephone (714) 856-4715; E-mail address: PJBRYANT@UCI; Fax number: (714) 856-7399. In the cover letter to the Editor or on the manuscript title page, indicate the name, address, and telephone number of the author who should be contacted in editorial matters.

For information about advertising in *Developmental Biology,* please contact Calvin Caldwell, Advertising Coordinator, Journal Promotion Department, Academic Press, Inc., 1250 Sixth Avenue, San Diego, California 92101 (telephone: (619) 230-1840).

SOCIETY FOR DEVELOPMENTAL BIOLOGY, INC.

BOX 40741
WASHINGTON, D.C. 20016

NOMINATION FOR MEMBERSHIP

Excerpt from the Bylaws and the Code of the Society: "Election of a person to full or student membership shall be the Board of Trustees upon nomination by one sponsor who is a full member of the Society." "A doctoral degree or its equivalent and an interest in development and growth in biological systems shall be prerequisites for full membership." "Students enrolled in a graduate program leading to an advanced degree in Developmental Biology or related fields shall be eligible for student membership."

Membership Category: _____Full _____Student

Name of Candidate: _____

Degrees, granting institutions and dates:

_____

_____

_____

Present position: _____

Current mailing address (no name) (three lines of 30 characters each for address label)

_____

_____

_____

Telephone number (area code, number and extension, if any) _____

Signature of one sponsor who is a full member of the Society:

Name _____ Signature _____

Address _____

Additional Instructions:

1. Please do not submit dues with this application.
2. Return the completed application to:

   Society for Developmental Biology, Inc.
   Box 40741
   Washington, DC 20016

3. Please use the back of this form to describe your major professional interests.

Subscriptions to DEVELOPMENTAL BIOLOGY are now included with membership.